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NEW RECORDS OF *SCOLELEPIS* (POLYCHAETA: SPIONIDAE) FROM THE SANDY BEACHES OF MADAGASCAR, WITH THE DESCRIPTION OF A NEW SPECIES

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ABSTRACT

Three species of the genus *Scolelepis* (Polychaeta, Spionidae) are reported from intertidal beaches in Madagascar. A new species, *Scolelepis* (*Scolelepis*) *vazaha* n.sp., is described from Cap Est (type locality) and Fort Dauphin. This species is unique among spionids in possessing at least one large, curved hook in each notopodium of setiger 4. Males may additionally have similar hooks on setiger 5 or on setigers 5 and 6. On median setigers males also possess peculiar notopodial swellings, some of which contain a geniculate, penicillate seta of a type previously unknown for the family. *S.* (*S.*) *williami* (de Silva, 1961), formerly known only from the original description of two specimens from Sri Lanka, was found on five beaches along the southeast coast of Madagascar. This poorly known species is redescribed and compared to the closely related *S.* (*S.*) *laciniata* Eibye-Jacobsen, 1997, described from the west coast of Thailand. *S.* (*S.*) *lefebvrei* (Gravier, 1905), previously reported from the west coast of Madagascar, was also found on six sandy beaches along the northeast and southeast coasts. Earlier descriptions are supplemented by information on variation in numerical characters. Scanning electron photographs and details on palp morphology are provided for all three species.

Surprisingly few named species of Spionidae have previously been reported from Madagascar. Fauvel (1919) cited *Polydora ciliata* (Johnston, 1838) from Tuléar on the SW coast of the island. Day (1962) reported *Scolelepis* (*Scolelepis*) *cirratulus* (as *Nerine* = *S.* (*S.*) *squamata* (Müller, 1806) fide Maciolek, 1987) and *S.* (*S.*) *lefebvrei* (Gravier, 1905) (also as *Nerine* and mistakenly referred to Gravier, 1906) from Nossi-Bé, NE Madagascar. Both latter species were later found at sandy beaches near Tuléar as well (Pichon, 1967).

Pichon (1967) wrote that she had some doubt in identifying her animals as *Nerine cirratulus*. This species, i.e., *S.* (*S.*) *squamata*, has been widely reported from the Atlantic and Indian Oceans, as well as from along the Pacific coast of Canada and the United States. The issue of whether one or more species are involved is a subject that we hope to address in a future publication, based on newly collected material from Brazil, Madagascar and Thailand.

The material reported on in this paper was collected by the second author in connection with his Ph.D. studies which entail an investigation into the influence of beach morphodynamics and latitudinal gradients on the biodiversity of sandy beaches. Most of the spionids collected in Madagascar have been lost, because in the context of the thesis it was necessary to determine their ash-free dry weight. Such animals are not included in the taxonomic accounts below but information on them is included under the Distribution and Ecology sections. Fortunately, a considerable number of animals were spared as voucher specimens. Three species were found in the material, including one new to science and one that was previously known in little detail only. These species provide significant contributions to our knowledge of the taxonomy of *Scolelepis* and are described below.

Materials and Methods

Eleven beaches were sampled on the east coast of Madagascar. On each beach, 15 stations were established along a transect perpendicular to the shore line running from the base of the fore dunes to the lowest level of the swash zone. In some coral reef beaches without a swash zone, some stations were also established in the upper sublittoral. At each station, triplicate 0.1 m^2 sand samples were taken to a depth of 25 cm with a metalic core sampler. The sand was sieved through a 1 mm mesh net. More complete information on the sampling schemes used and a full description of the sampling sites will be provided in a future paper on the ecology of polychaetes from the sandy beaches of Madagascar.

The non-parametric Mann-Whitney U test was used to test the significance of body size differences between males and females of *Scolelepi* (*Scolelepis*) *vazaha* n.sp.

Material has been deposited at the following institutions: Zoological Museum, University of Copenhagen, Denmark (ZMUC); South African Museum, Cape Town (SAM); Australian Museum, Sydney (AM); Centro de Estudos do Mar, Universidade Federal do Paraná, Brazil (MCEM); Natural History Museum of Los Angeles County, Los Angeles (LACM-AHF); Natural History Museum, London (NHM); National Museum of Wales (NMW); Naturhistoriska Riksmuséet, Stockholm (SMNH); Smithsonian Institution, Washington D.C. (USNM).

Taxonomy

Scolelepis* (*Scolelepis*) *vazaha new species
(Figs. 1–3)

Material Examined.—Cap Est, northeast Madagascar, 15°18′S, 50°29′E (type locality), sta. 15B, 11 March 1996, at low intertidal (saturation zone) of a low energy reflective beach protected by a coral reef 500 m offshore (ZMUC POL-962, holotype; ZMUC POL-963, 29 paratypes, including two mounted on SEM-stubs; SAM A21460, 3 paratypes; AM W25338, 2 paratypes; MCEM BPO-1219, 2 paratypes; LACM-AHF 1903, 2 paratypes; NHM 1999.546-547, 2 paratypes; NMW.Z.1999.014.3, 2 paratypes; SMNH 5096, 2 paratypes; USNM 185991, 2 paratypes). Fort Dauphin, Baie de Libanona, southeast Madagascar, 25°2′S, 46°58′E, sta. 14C, 3 March 1996, at low intertidal (saturation zone) of a high energy exposed dissipative beach (ZMUC POL-964, 10 spec., including two mounted on SEM-stubs).

Description.—Holotype anterior fragment of female with 29 setigers, 5.8 mm long, 0.8 mm broad excluding setae. No complete specimens observed; anterior fragments up to 7.3 mm long, with up to 46 setigers. Comparisons of anterior and posterior fragments indicate that at least 70 setigers may be present, with total length of about 14 mm. Body anteriorly dorso-ventrally compressed, becoming distinctly narrower, almost cylindrical in cross section from around setiger 22 (Fig. 2H). Median and posterior part of body fragile, prone to fragmentation. Preserved animals uniformly light orange brown; pigmentation of living animals unknown.

Anterior end of prostomium strongly acute (Figs. 1A,2A); posterior end broadly triangular, slightly raised, without occipital antenna or obvious caruncle, extending to setiger 2. Two pairs of small reddish brown eyes present, anterior eyes slightly larger than posterior ones (Fig. 1A). Peristomium forming weak lateral wings around base of prostomium (i.e., closely apposed to prostomium but not fused with it, Figs. 1A,2C). Proboscis not observed. Palps relatively short, not easily detached, up to 1.3 mm long; ciliation consists

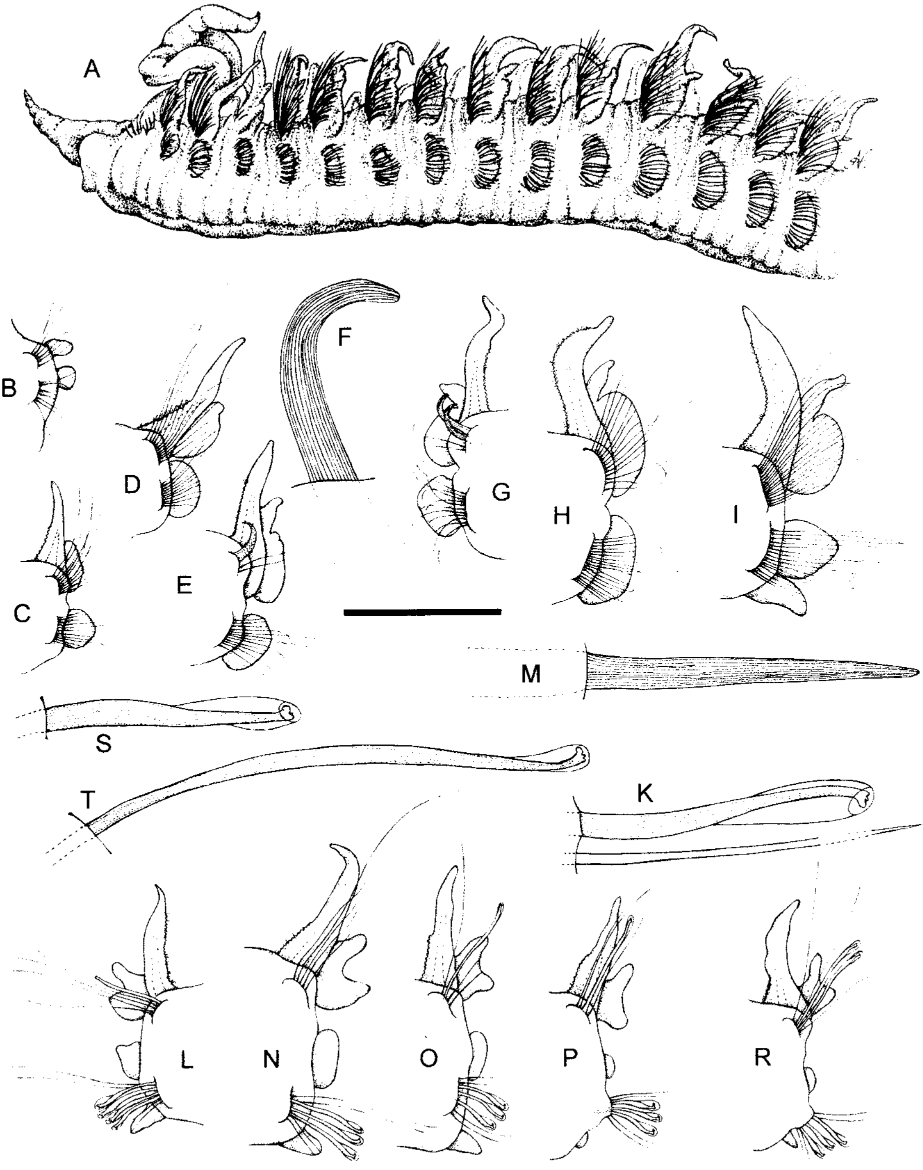

Figure 1. *Scolelepis* (*Scolelepis*) *vazaha* n.sp. A: Anterior end, lateral view, holotype. B-M: Parapodia and setae of female paratype (ZMUC-POL-963). B: Parapodium of setiger 1. C: Parapodium of setiger 2. D: Parapodium of setiger 3. E: Parapodium of setiger 4, showing large notopodial hook. F: Notopodial hook from setiger 4. G: Parapodium of setiger 4 with two notopodial hooks. H: Parapodium of setiger 10. I: Parapodium of setiger 20. K: Neuropodial hooded hook and companion seta of setiger 30. L: Parapodium of setiger 35. M: Hook from notopodium in L, reduced hood not shown. N-T: Parapodia and setae from posterior fragment (ZMUC-POL-963). N: Parapodium taken 32 setigers anterior to pygidium. O: Parapodium 16 setigers anterior to pygidium. P: Parapodium 10 setigers anterior to pygidium. R: Parapodium 4 setigers anterior to pygidium. S: Neuropodial hooded hook from parapodium in R. T: Notopodial hooded hook from parapodium 5 setigers anterior to pygidium. All parapodia shown in anterior view. Scale = 0.5 mm for A, 0.25 mm for parapodia (B–E, G–I, L, N–R) and 50 μm for setae (F, K, M, S, T).

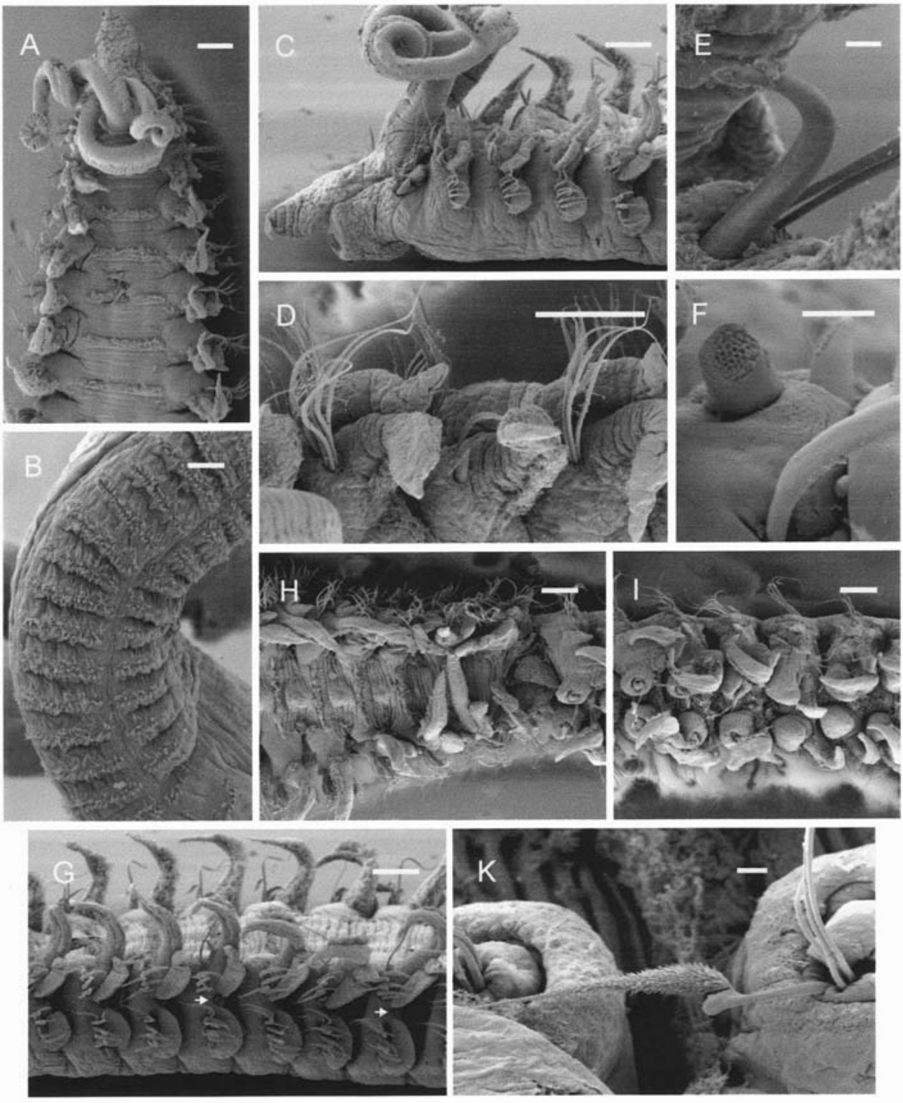

Figure 2. *Scolelepis* (*Scolelepis*) *vazaha* n.sp. SEM micrographs. A: Anterior end, dorsal view. B: Middle section of palp showing pattern of ciliation. C: Anterior end, lateral view. D: Notopodia of setigers 3–5, lateral view. E: Enlarged hook from notopodium of setiger 4, dorsal view. F: Broken notopodial hook from setiger 4 showing inner microvillar structure of central cortex and peripheral medulla. G: Setigers 5–11, dorsolateral view (arrows indicate interramal ciliated organs). H: Setigers 17–23, dorsal view, showing sharp narrowing of body. I: Setigers 23-28, dorsal view, showing notopodial swellings. K: Geniculate penicillate notoseta from setiger 23. ZMUC-POL-963 (female: D, E) and ZMUC-POL-964 (female: A, C, F, G; male: B, H–K). Scale = 10 µm for B, E, F and K, 100 µm for all other figures.

of two longitudinal bands of transverse rows of cilia (Fig. 2B). Each row in median band up to 30 µm long, in lateral band up to 20 µm long; ciliary groove absent. Palp sheaths short, slightly rugose, fused to base of palps. Nuchal organs at posteromedian base of palps.

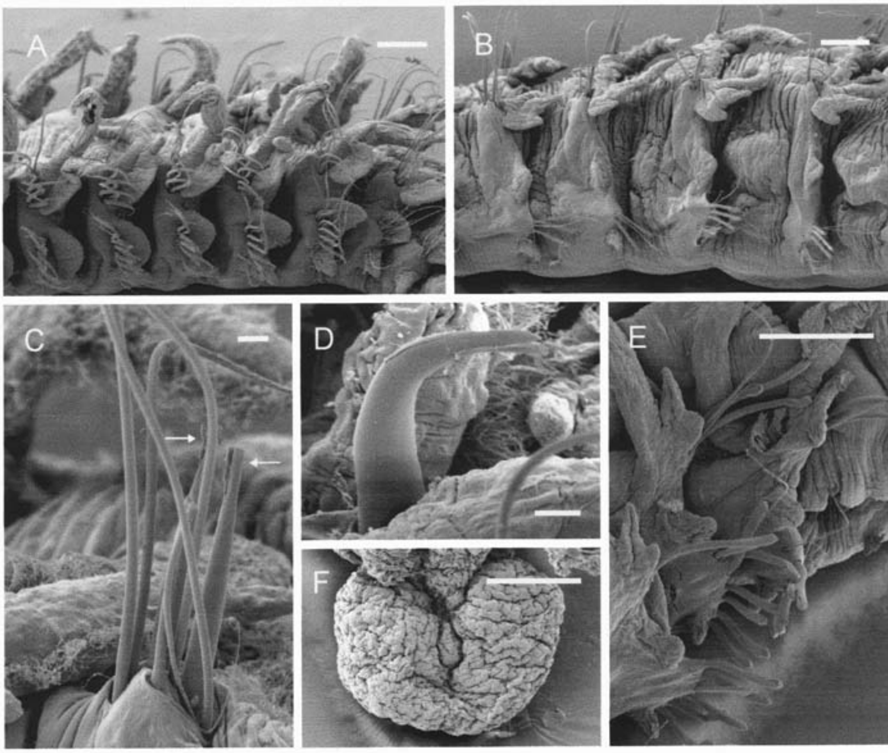

Figure 3. *Scolelepis* (*Scolelepis*) *vazaha* n.sp. SEM micrographs. A: Setigers 17-22, lateral view, showing gradual subdivision of neuropodial postsetal lamella (note: subdivision has already begun on setiger 17, at left). B: Setigers 29-32, lateral view, showing hooded neuropodial and weakly hooded notopodial hooks beginning on same setiger. C: Notopodium of setiger 36 showing two notopodial hooks with reduced hoods (arrows). D: Curved hook with reduced hood from setiger 40 (note strong resemblance to notopodial hook of setiger 4, compare Fig. 2E). E: Posterior parapodium (5 setigers anterior to pygidium), posterior view, with neuropodial and notopodial hooded hooks. F: Pygidium (damaged), dorsal view. ZMUC-POL-963 (posterior fragment, F) and ZMUC-POL-964 (female: A–C; male: D; posterior fragment: E). Scale = 10 μm for C and D, 100 μm for all other figures.

Gills present from setiger 2 to end of body, apart from on the first few setigers of uniform length throughout. Gills fused basally to notopodial postsetal lamellae (e.g., Fig. 2G); each gill with band of cilia along inner edge (Fig. 2D); each segment also with dorsal, transverse band of cilia, not continuous with ciliation of gills (Fig. 2A).

Parapodia of setiger 1 small but well-developed; notopodium with capillary setae and postsetal lamella (Fig. 1B). Neuropodial postsetal lamella rounded on anterior setigers (Fig. 1B–E,G,H), developing notch dividing lamella into larger dorsal and smaller ventral lobe from about setiger 15 (Fig. 3A). Notch becoming deeper, dividing lamella into separate lobes by setiger 23 (Fig. 1I,3A); on following setigers ventral lobe remaining bluntly triangular, located ventral to neurosetae; dorsal lobe broadly triangular to about setiger 35, subsequently rounded rectangular, placed midway between neuro- and notosetae (Fig. 1L,N–R). Notopodial postsetal lamella developing small notch on setiger 3 (Fig. 1D), gradually increasing in size and dividing lamella into two lobes; ventral lobe large and

rounded (Fig. 1H,I), decreasing in size and becoming more drawn out from about setiger 25; dorsal lobe elongate, best developed on setigers 8–25 (Fig. 1H,I).

Neurosetae in two rows, most apparent on anterior setigers. Neuropodia of anterior setigers with capillaries only, those of anterior row broadest, weakly bilimbate, shorter than those of posterior row. Neuropodial hooded hooks from setiger 25–31 (n = 34, on 25 of these specimens hooks start on setiger 27–29), up to 7 present per neuropodium, present to end of body. Hooded hooks distally tridentate, with bluntly rounded main fang surmounted by two smaller accessory teeth placed side by side (Fig. 1K,S). With the appearance of hooded hooks the capillary neurosetae become narrower and reduced in number (companion setae), typically with two long setae above and two short setae below the hooks (Fig. 1L–P). Well developed interramal ciliated organ (lateral organ) present between neuropodium and notopodium of all parapodia (Fig. 2G).

Notopodial capillary setae similar in morphology to those of neuropodia although more elongate, arranged in two rows, those of posterior row longest. Notopodia of setiger 4 with only 1–3 capillary setae and one large (up to 15 μm thick), strongly curved, distally blunt spine (Figs. 1F,2E); spine placed dorsally in notopodial fascicle (Figs. 1E,2D). Two spines may be present on one side of the body (Figs. 1G,2F). Most males with similar hooks additionally on setiger 5 or setigers 5 and 6 (see Remarks).

Notopodial hooks with reduced hoods (Fig. 3C,D), starting on same setiger as neuropodial hooded hooks or 1–2 setigers posterior to this (Fig. 1L), only one or two per notopodium (Fig. 3C). These hooks straight at first (Fig. 1M), gradually becoming more strongly curved by about setiger 40 (Fig. 3D); at this point hooks strongly resemble those of setiger 4 in shape and size, except for reduced hood (compare Fig. 2E with 3D). On following 3–5 setigers notopodial hooks reduced in length and less curved distally (this region only present on few anterior and two posterior fragments); next 10–15 setigers with capillary notosetae only (Fig. 1N). Posterior 10–16 setigers with 1–3 hooded hooks per notopodium (Fig. 1O–R); notopodial hooded hooks similar to those of neuropodia, tridentate, but narrower and more elongate (Figs. 1T,3E).

Males with unusual development of notopodia on middle region of body: From setiger 22–23, where body becomes narrow and more cylindrical, following 9–10 pairs of notopodia suddenly strongly swollen, apically glandular, with setae emerging through tip on first 2–3 of these setigers, subsequently emerging at base of swelling (Fig. 2H,I). On setigers with notosetae emerging through tip of notopodial swelling, one of these notosetae stout, geniculate, with penicillate terminal portion (Fig. 2K); these setae absent in all other notopodia (and entirely absent in females).

Males with well developed dorsal organs on setigers 11–20 (Fig. 2H, at left).

Pygidium circular in outline but dorsoventrally flattened, with dorsal longitudinal indentation (Fig. 3F).

Several females with almost mature eggs, up to 120 μm in diameter, from setiger 23. Some males with sperm in same region.

Tube fragments observed, very fragile, consisting of thin layer of mucus with adhering sand grains.

Etymology.—The species epithet *vazaha* (pronounced vazá) is a Malagasy word for ‘foreigner’ or ‘stranger’, a reference to the several characters of this species that were previously unknown for the genus *Scolelepis*, most importantly the large notopodial spines of setiger 4.

Remarks.—*S*. (*S*.) *vazaha* exhibits several characters that are unique for *Scolelepis* and indeed among spionids in general: (1) enlarged notopodial spines on setiger 4; (2) the median region displaying notopodial hooks with reduced hoods, separated from the posteriormost region (with 'normal' notopodial hooded hooks) by a number of setigers without notopodial hooks of any kind; and (3) the peculiar notopodial swellings in males, each with a geniculate, penicillate seta on setigers 23–25. The question arose as to whether a new genus should be erected for this species, but such action would clearly be indefensible because the species possesses the specific autapomorphies of *Scolelepis*: (1) palps with reduced ciliation and lacking a ciliary groove; (2) the subdivision of the neuropodial postsetal lamellae on median setigers; and (3) a spherical pygidium without cirri or lobes (shared with at least some species of *Dispio*). *S*. (*S*.) *vazaha* also shares all the more general characters of *Scolelepis*, most importantly the shape of the prostomium, the distribution of gills, and the morphology of the neuropodial hooded hooks. Thus, the unusual characters of the new species, however exceptional, have evolved as further developments in a lineage that was already clearly a member of *Scolelepis*.

The propensity of individuals of this species to fragment, most often somewhere between setigers 25 and 35, created problems in providing a complete description. We considered disregarding all posterior fragments completely, especially since the picture that arose regarding the distribution of notopodial hooks with reduced and complete hoods was so unusual. The linkage between anterior and posterior fragments was supported by the numbers and sizes of both in the material and the fact that the only other species present in the same samples that could be the source of the posterior fragments, *S*. (*S*.) *lefebvrei*, has unidentate neuropodial hooded hooks that are easily distinguished from those of the new species. The compelling argument, however, is the fortunate presence in the material of two posterior fragments (ZMUC-POL-963 and ZMUC-POL-964) long enough to include the most posterior setigers that have notopodial hooks with reduced hoods, the following setigers without notopodial hooks, and the final setigers with "normal" notopodial hooded hooks. All fragments in the material are consistent with the description provided above.

S. (*S*.) *vazaha* provides yet another example of a spionid in which certain setae on anterior setigers have become particularly stout. The best known examples are the notopodial spines on setiger 5 of species in the *Polydora* complex and the neuropodial hooks on setiger 1 in *Spiophanes*. Several other cases have recently been described: *Australospio trifida* with thickened capillaries in the neuro- and notopodia of setigers 6–9 (Blake and Kudenov, 1978), *Microspio paradoxa* with thickened capillary setae in the notopodia of setigers 4 and 5 (Blake, 1983), *Scolecolepides uncinatus* with acicular spines in the neuropodia of setigers 9–18 (Blake, 1983), and *Lindaspio dibranchiata* and *L. southwardorum* with the notosetae of setigers 2–4 modified as clusters of heavy spines (Blake and Maciolek, 1992). It appears that most or all of these modifications have arisen independently of one another, which raises the question as to whether this has taken place as a response to similar or different environmental pressures, such as the need for species specific pair formation. Without more detailed knowledge on the actual significance of these setae to the animals themselves, any hypothesis would be idle speculation at this time.

S. (*S*.) *vazaha* is unusual in exhibiting sexual dimorphism. Males have swollen notopodia from setiger 22–23 to setiger 28–30 and dorsal organs on setigers 11–20 (which presumably aid them in locating ripe females). Females containing eggs lack these swellings and

dorsal organs. Twenty-five males were identified among a total of 55 anterior ends (the remaining two being too short to allow sex determination). Notopodial swellings began on setiger 23 in 18 of these animals and on setiger 22 in the other seven. The number of setigers on which the notosetae (including the odd geniculate, penicillate seta) emerge from the top of the swelling is 3 in most specimens, only three animals having them limited to 2 setigers.

Another indication of sexual dimorphism is the tendency for males to have additional notopodial spines on setigers 5 and 6. Females without exception have these spines limited to setiger 4, whereas eleven males have them on setigers 4 and 5 and eight have them on setigers 4, 5 and 6. The exact nature of this variation and how it relates to the separation of males and females is unclear, as the remaining six males were similar to females in having notopodial spines on setiger 4 only (there is no clear correlation between the size of a male and the number of setigers with spines). What is even more unclear is the function of the notopodial spines of both sexes and the notopodial swellings of males, although it is reasonable to speculate that they could be employed in some type of pseudocopulation. Observations on living specimens of *S.* (*S.*) *vazaha* would obviously be of great interest to specialists in polychaete reproductive biology. As a final indication of sexual dimorphism, it was observed that males are slightly smaller than females, as judged by body width at setiger 8, excluding setae (averages of 0.62 and 0.68 mm, respectively). Thus, the Mann-Whitney U test of whether two median values are significantly different produces a statistic ($U = 2.58$) that is significant at the 1% level.

Apart from the occurrence of dorsal organs, reports of sexual dimorphism in spionids are rare. The only other cases that we are aware of concern the genera *Pygospio*, *Pygospiopsis* and *Pseudopolydora* (Blake, 1983) in which males of some species have gill distributions different from females.

The possession of large notopodial spines on setiger 4 distinguishes *S.* (*S.*) *vazaha* from all other species of the genus (similar, so-called ‘boathooks’ may be found in the notopodia of posterior setigers in species of *Boccardiella*, see Blake, 1983). The presence of a median body zone in which there are notopodial hooks with reduced hoods is also unique (note that the notopodial hooks of setigers 4–6 are always distally entire, reducing the likelihood that the reduced hoods observed on middle setigers are artifacts), although neuropodial hooks with reduced hoods are known for *S.* (*S.*) *eltaninae* Blake, 1983. Blake and Kudenov (1978) reported that unhooded notopodial acicular spines were present in median and posterior setigers of a new species from Queensland, *S.* (*S.*) *viridis*. It should be noted that the presence of reduced hoods on the notopodial hooks on median setigers of *S.* (*S.*) *vazaha* had to be confirmed by the use of SEM. Thus, the possibility exists that the spines described for *S.* (*S.*) *viridis*, known only from light microscopical observations, also have reduced hoods.

Distribution and Ecology.—*S.* (*S.*) *vazaha* is only known from Madagascar, from the northeast (15°12′S, 50°26′E), including beaches in Baie D’Antongil (15°30′S, 49°39′E), to the southeast (25°2′S, 46°58′E), on beaches around Fort Dauphin. It inhabits the upper sublittoral (surf zone) and lower intertidal (saturation zone) of low energy reflective, intermediate and high energy dissipative beaches. It was found in densities of up to 132 ind m^{-2}, corresponding to a biomass of 126 mg m^{-2}.

Scolelepis (*Scolelepis*) *williami* (de Silva, 1961)
(Figs. 4–5)

Nerinides williami de Silva, 1961: 183-184; fig. 9.
Scolelepis (*Scolelepis*) *williami*. — Maciolek, 1987: 19.

Material Examined.—Madagascar**:** Cap Est, NE Madagascar, 15°18′S, 50°29′E, sta. 8B, 11 March 1996, at mid intertidal (retention zone) of a low energy reflective beach (ZMUC POL-958, 39 spec., including two mounted on SEM-stubs). Fort Dauphin, Baie de Libanona, SE Madagascar, 25°2′S, 46°58′E, sta. 8A, 3 March 1996, at mid intertidal (retention zone) of a high energy exposed dissipative beach (ZMUC POL-959, 54 spec.; ZMUC POL-961, 1 spec.; SAM A21459, 3 spec.; AM W25336, 2 spec.; MCEM BPO-1220, 2 spec.; LACM-AHF, 2 spec.; NHM 1999.550-551, 2 spec.; NMW.Z.1999.014.2, 2 spec.; SMNH 16881, 2 spec.; USNM 185992, 2 spec.). Fort Dauphin, Ambinanibe, SE Madagascar, 25°5′S, 46°56′E, sta. 5A, 4 March 1996, at mid-high intertidal (retention zone) of a high energy exposed intermediate beach (ZMUC POL-960, 1 spec.).

Sri Lanka**:** Kathaluwa, South Province, 1960?, fine sand, coll. P. H. D. H. de Silva (NHM 1962.14.3, paratype).

Description.—(This description is based on specimens from Madagascar unless otherwise stated.) Animals up to 38 mm long, 1.4 mm broad excluding setae, with up to 98 setigers. Middle and posterior segments slightly more elongate than anterior ones. Body almost rectangular in cross section. Preserved animals uniformly light brown (paratype dark brown). Living animals red and black (de Silva, 1961).

Anterior end of prostomium acute, pointing forward and slightly downwards; posterior end also acute, raised as a high crest but without occipital antenna or caruncle, reaching middle of setiger 2 (Figs. 4A,5A,B). Two small pairs of reddish brown eyes, anterior pair largest (not apparent on Fig. 4A). Peristomium enveloping prostomium and closely apposed to it, not forming lateral wings (Figs. 4A,5A). Proboscis strongly ciliated (Fig. 5A). Palps slender and elongate, quite easily detached; ciliation consists of two longitudinal bands of transverse rows of cilia. Each row in median band 20 μm long near base and up to 35 μm long on middle part of palp; each row in lateral band only 7 μm long near base and up to 20 μm long on middle part of palp; ciliary groove absent (Fig. 5C–F). Palp sheaths short, with smooth edge, without adornment, fused to base of palps (Fig. 5A). Nuchal organs well developed, crescent-shaped, at posteromedian base of palps (Fig. 5B).

Gills present from setiger 2 to end of body, longest on anterior and middle part of body; partially fused to notopodial postsetal lamellae but with at least terminal half free throughout (Fig. 4C–H,L). Each gill with band of cilia along inner edge (Fig. 5G). Weakly developed transverse band of cilia present across dorsum of most setigers, not continuous with ciliation of gills, absent on last 10–15 setigers of body. Low dorsal fold across each setiger from about setiger 30 (Fig. 5I). Tip of gill with up to 4 clavate papillae from setiger 17–20 to 39–42 (Figs. 4F–G,5G), tip of each papilla strongly ciliated (Fig. 5H).

Parapodia of setiger 1 weakly developed; notosetae absent but notopodial postsetal lamella present (Fig. 4B,5B); neuropodium with only 3–5 short capillary setae. Neuropodial postsetal lamella rounded on anterior setigers (Fig. 4C–E), developing a notch on setiger 17 (Fig. 4F) which completely divides lamella into two lobes by setiger 22 (Fig. 4G). Distance between lobes increasing on subsequent setigers, the dorsal lobe being midway between neuro- and notosetae on posterior half of body; both lobes very small and rounded

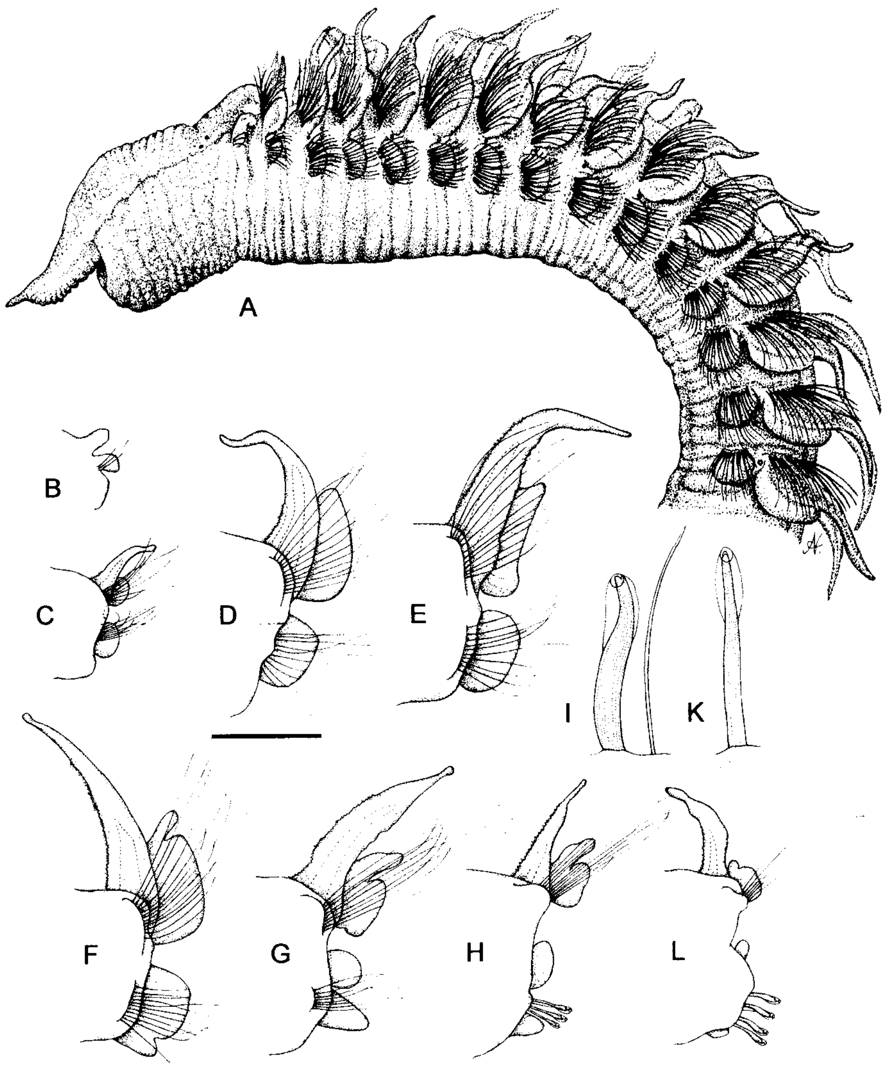

Figure 4. *Scolelepis* (*Scolelepis*) *williami* (de Silva, 1961). A: Anterior end, lateral view, palps removed, specimen from ZMUC-POL-958. B-L: Parapodia and setae of another specimen from same lot. B: Parapodium of setiger 1. C: Parapodium of setiger 2. D: Parapodium of setiger 6. E: Parapodium of setiger 11. F: Parapodium of setiger 19. G: Parapodium of setiger 30. H: Parapodium of setiger 40. I: Hooded hook and companion seta from neuropodium of setiger 70, lateral view. K: Hooded hook from neuropodium of setiger 40, dorsal view. L: Parapodium of setiger 70. All parapodia shown in anterior view. Scale = 0.5 mm for A, 0.25 mm for B-H and L and 50 μm for I and K.

on posterior setigers (Fig. 4H,L). Notopodial postsetal lamella rounded on anterior setigers, developing drawn out dorsal tip from setiger 5 (Fig. 4E) and dorsal notch from about setiger 15 (Fig. 4F–H), strongly reduced on posterior setigers (Fig. 4L).

Neuropodia of anterior setigers with capillaries only. Neuropodial hooded hooks beginning on setiger 36–38, up to 6 per neuropodium, present to end of body (Fig. 4H,L). Hooded hooks distally bidentate (Fig. 4I, K). Well developed interramal ciliated organs

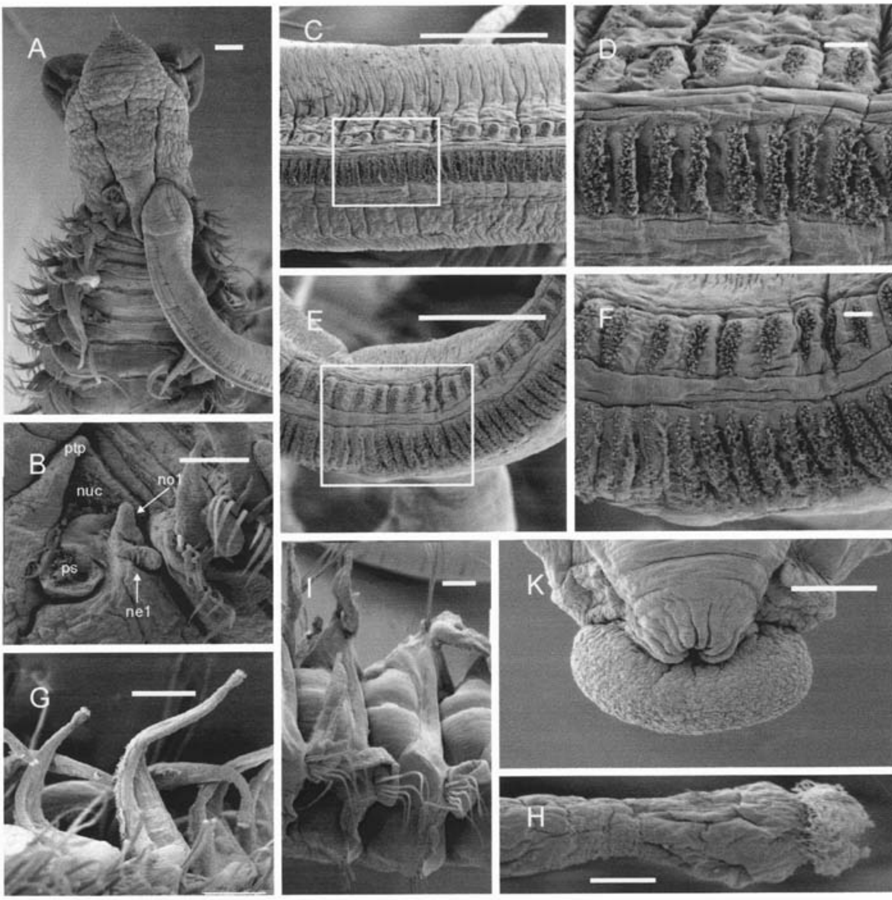

Figure 5. *Scolelepis* (*Scolelepis*) *williami* (de Silva, 1961). SEM micrographs. A: Anterior end, dorsal view. B: Detail of area around parapodium of setiger 1 (ne1 = neuropodium of setiger 1, no1 = notopodium of setiger 1, nuc = nuchal organ, ps = palp scar, ptp = posterior tip of prostomium). C: Portion of palp near base. D: Detail of area indicated in C. E: Portion of palp halfway along its length. F: Detail of area indicated in E. G: Gills of setigers 17–20 showing terminal clavate swellings. H: Detail of gill tip from setiger 28. I: Dorsolateral view of setigers 77–79 (from complete specimen with 92 setigers). K: Pygidium, dorsal view. ZMUC-POL-958 (2 specimens and a posterior fragment). Scale = 10 µm for D, F and H, 100 µm for all other figures.

(lateral organs) present between neuro- and notopodium of all parapodia. All notosetae capillaries.

Pygidium with large, broad ventral cushion and dorsally placed anus (Fig. 5K).

Remarks.—*S*. (*S*.) *williami* was originally described on the basis of two specimens taken on a sandy beach in southern Sri Lanka. The present specimens from Madagascar were carefully compared with the paratype (NHM 1962.14.3), which is 64 mm long and has 100 setigers, i.e., slightly smaller than the holotype, which according to de Silva (1961) is 72 mm long with 103 setigers. The largest specimen from Madagascar is 38 mm long with 98 setigers and thus presumably a subadult since there are no indications of sexual maturity in the animals newly reported on here.

There is total agreement in all details between the paratype and animals from Madagascar. For example, in both cases the neuropodial postsetal lamellae develop a notch on setiger 17 and separation into two lobes is complete on setiger 22. The paratype has clavate papillae on the gills of setigers 20–38 and neuropodial hooded hooks begin on setiger 36 on the right side and setiger 38 on the left side of the body (not posterior to setiger 40 as stated in the original description). These values are within the range of variation observed on specimens from Madagascar. The pygidial morphology is identical.

A striking similarity occurs in the relatively low number of hooded hooks per neuropodium in this large species, the maximum number observed being 6. De Silva stated that up to 8 hooded hooks are present (see also his fig. 9f), but on the paratype at least, this is not the case.

The specimens from Madagascar differ slightly from the paratype in the maximum number of clavate gill papillae (4 and 6 per gill, respectively). This difference can probably be assigned to the fact that the animals from Madagascar are smaller and not quite mature.

S. (*S.*) *williami* closely resembles *S.* (*S.*) *laciniata* Eibye-Jacobsen, 1997, described from similar habitats on the west coast of Thailand. They are the only species of *Scolelepis* for which clavate gill papillae have been described. The two species may, however, be separated on several characters: in *S.* (*S.*) *laciniata* setiger 1 not only lacks notosetae but also notopodial postsetal lamellae; clavatae papillae are relatively larger and not as strongly concentrated on the apical part of the gill as in *S.* (*S.*) *williami*, as well as being absent beyond setiger 28; notopodial postsetal lamellae on setigers 11–28 have up to five lateral lobes, absent in *S.* (*S.*) *williami*; neuropodial hooded hooks begin further forward on the body, on setiger 24–26, and number up to 10 per neuropodium; the pygidium is almost spherical, whereas it is decidedly broader than long in *S.* (*S.*) *williami*.

Dauer (e.g., 1985 and 1987) has pointed out that the palps of members of *Scolelepis* (possibly only shallow water species) are unusual among spionids in lacking a ciliary food groove and in having non-motile cilia only, arranged in two longitudinal bands of transverse rows. The pattern of ciliation described above for *S.* (*S.*) *vazaha* and below for *S.* (*S.*) *lefebvrei* agree with Dauer's observations on, e.g., *S.* (*S.*) *squamata* (Müller, 1806). The palps of *S.* (*S.*) *laciniata*, although also conforming to this pattern, are atypical in having reduced ciliation, the band with the shorter rows of cilia being present only as small ciliated cushions with a maximum length of 5 μm (see fig. 2d in Eibye-Jacobsen, 1997). We have since confirmed that this pattern exists along the entire length of the palp. The palps of *S.* (*S.*) *williami* are interesting in that they exhibit an intermediate condition. Thus, the pattern of ciliation at the base of the palp is very similar to that in *S.* (*S.*) *laciniata* (Fig. 5D), whereas it is closer to the pattern in other species of the genus along the rest of the palp (Fig. 5F), although still with considerably shorter transverse rows of cilia relative to the width of the palp itself. The functional significance of this reduced ciliation is not clear, but it certainly appears to be a further indication that *S.* (*S.*) *williami* and *S.* (*S.*) *laciniata* belong to a distinct clade within the subgenus.

Distribution and Ecology.—*S.* (*S.*) *williami* is known only from Sri Lanka (de Silva, 1961) and Madagascar (present paper), although it is reasonable to assume that it is more widely distributed in suitable habitats elsewhere in the Indian Ocean. Its distribution in Madagascar ranges from the northeast (15°12′ S, 50°26′ E), on beaches around Cap Est, to the southeast (25°5′S, 46°56′E), on beaches around Fort Dauphin. Its occurs intertid-

ally from low (resurgence zone) to mid shore (retention zone) on low energy reflective beaches, as well as on intermediate and high energy dissipative beaches, as mentioned for *S.* (*S.*) *vazaha*. It can also occur on coarser grained high energy reflective beaches. It reached densities of up 292 ind m^{-1}, corresponding to a biomass of 538 mg m^{-2}.

Scolelepis (*Scolelepis*) *lefebvrei* (Gravier, 1905)
(Fig. 6)

Nerine lefebvrei Gravier, 1905: 43-44.
Nerine lefebvrei. — Gravier, 1906: 159–162; figs. 322–326; pl. 2, fig. 185. Fauvel, 1919: 427–428. Day, 1962: 648. Pichon, 1967: 75, 83, 87, 91, table 2.
Scolelepis (*Scolelepis*) *lefebvrei*. Maciolek, 1987: 18. Imajima, 1992: 10–13; figs 6–7.

Material Examined.—Cap Est, NE Madagascar, 15°18′S, 50°29′E, sta. 13B, 11 March 1996, at mid-low intertidal (resurgence zone) of a low energy reflective beach protected by a coral reef 500 m offshore (ZMUC POL-957, 1 spec.). sta. 15B, as previous station, low intertidal, saturation zone (ZMUC POL-956, 32 spec., including two mounted on SEM-stubs; SAM A21458, 3 spec.; AM W25337, 2 spec.; MCEM BPO-1221, 2 spec.; LACM-AHF, 2 spec.; NHM 1999.548-549, 2 spec.; NMW.Z.1999.014.1, 2 spec.; SMNH 16882, 2 spec.; USNM 185993, 2 spec.).

Remarks.—The original description of this species, in combination with Gravier's (1906) subsequent more thorough report, was quite detailed and recently Imajima (1992) has given an excellent description of a specimen from Japan. There is thus no need to provide a full description here, only to point out a few minor points of divergence and, on the basis of the rather large number of specimens available for study, to provide some information on variation within the population from Madagascar.

The material from Madagascar consists mainly of anterior fragments. The largest specimen is 2.0 mm broad (excluding setae), i.e., considerably smaller than the sizes reported by Gravier and Imajima (3 and 3.2 mm, respectively). They agree in all diagnostic characters with the descriptions provided by these authors, including having the four eyes arranged in almost a transverse row, well developed notopodia on setiger 1 (Fig. 6A–D), neuropodial hooded hooks that are unidentate (Fig. 6H) and glandular tips on the gills of anterior and median setigers (Fig. 6G).

Some small discrepancies can probably be explained by the fact that the animals from Madagascar are not quite mature. Thus, neuropodial hooded hooks begin on setiger 32–37 (n = 20), whereas both Gravier and Imajima reported that they begin on setiger 38. Similarly, Imajima mentioned that a notch appears on the neuropodial postsetal lamella on setiger 26, but on the specimens reported on here it starts on setiger 22–26 (n = 20). The lamella is divided into two lobes separated by a distinct gap 8 setigers posterior to the first appearance of the notch, after which the larger upper lobe becomes highly glandular.

There is one point in which a qualitative difference may be present. Imajima (1992) described the pygidium of *S.* (*S.*) *lefebvrei* as having an incised ventral cushion. The few pygidia in the material from Madagascar lack such an incision (Fig. 6I), in agreement with the original description of the species. More material from Japan must be studied before any conclusions can be reached as to whether this difference is significant.

The ciliation pattern on the palps of *S.* (*S.*) *lefebvrei* has not been described earlier. As shown on Figure 6E–F, it is consistent with the pattern generally observed in *Scolelepis*:

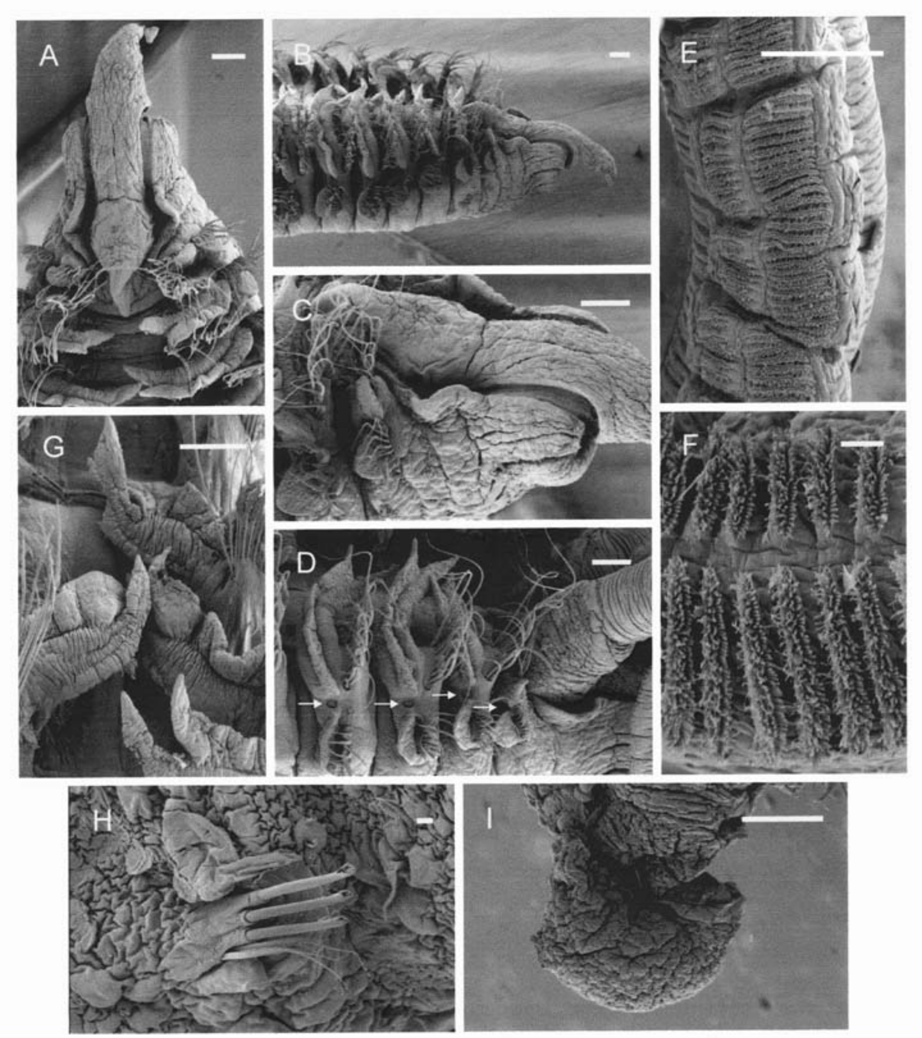

Figure 6. *Scolelepis* (*Scolelepis*) *lefebvrei* (Gravier, 1905). SEM micrographs. A: Anterior end, dorsal view. B: Anterior end, dorsolateral view. C: Detail of area around parapodium of setiger 1. D: Setigers 1–4, lateral view (arrows indicate interramal ciliated organs). E: Portion of palp halfway along its length. F: Detail of area shown in E (different angle). G: Setigers 30–32, anterodorsal view, showing expanded glandular tip of gills. H: Neuropodium of posterior setiger, lateral view. I: Pygidium (damaged), dorsal view. ZMUC-POL-956 (2 specimens and a posterior fragment). Scale = 10 μm for F and H, 100 μm for all other figures.

lacking a ciliary groove but having two longitudinal bands, each consisting of closely set transverse rows of non-motile cilia. The rows of cilia in the lateral band are up to 35 μm long and those of the median band are up to 55 μm long. These values are similar to those reported for *S.* (*S.*) *squamata* (see Dauer, 1987).

Distribution and Ecology.—*S.* (*S.*) *lefebvrei* is known from the Red Sea (Gravier, 1905, 1906; Fauvel, 1919), Madagascar (Day, 1962; Pichon, 1967; present paper) and Japan (Imajima, 1992). The material collected during this study was mainly found on beaches in the northeast part of the island, around Cap Est (15°12′S, 50°26′E), Baie D'Antongil

(15°30′S, 49°39′E) and the Masoala Peninsula (15°56′S, 50°9′E). Only one juvenile was found on a southern beach in Fort Dauphin. This species can be found from the upper sublittoral (surf zone), overlapping completely with *S.* (*S.*) *vazaha*, to the lower part of the retention zone where it overlaps with *S.* (*S.*) *williami*. *S.* (*S.*) *lefebvrei* was mainly found on low energy reflective and intermediate beaches. It reached its highest density, 169 ind m^{-2}, and biomass, 470 mg m^{-2}, on a low energy reflective beach fronted by a coral reef at Cap Est (15°18′S, 50°29′E) and its lowest density on a dissipative exposed beach.

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